

Anurans of Borjomi Canyon: clutch parameters and guild structure

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Spawn clutches of six anuran species, inhabiting Borjomi Canyon in central Georgia, were examined: *Rana macrocnemis*, *Bufo [bufo] verrucosistmus*, *Pelodytes caucasicus*, *Rana ridibunda*, *Bufo viridis* and *Hyla arborea*. The first three species constitute the guild of "Brown Anura" associated with forest and have the same spawning mode: females deposit a single clutch per year. The other three species prefer open areas and have multiple spawns. Brown Anura have larger eggs, and probably lower fecundity, than other amphibians of similar body size. Within the Brown Anura guild, different species show the same relationships of fecundity, egg size and clutch size with body length. Within the guild, lower fecundity and smaller eggs in species with smaller body size are compensated by rapid maturation. Among guilds, egg size is inversely correlated with fecundity.

INTRODUCTION

The reproductive success of amphibians is critically related to their pattern of spawning. Important variables include fecundity, egg size and total reproductive costs. Number of eggs per clutch (here and further: fecundity) relates to reproductive success in terms of the number of offspring, egg size in terms of their quality, reflected in the survivorship of larvae. Both developmental rates and hatchling size may depend on egg size (KAPLAN & COOPER, 1984, WALLS & ALTIG, 1986; WOODWARD, 1987; ISHCHEKNO, 1989; but see WALLS & ALTIG, 1986, KAPLAN, 1987; WILLIAMSON & BULL, 1989). Perhaps an increase of reproductive effort may result in a decrease in the survival rates of females, as in other animal groups (PARTRIDGE & HARVEY, 1985).

For the clutch characters, three alternative ways of adaptation might be favoured. an increase in egg number per clutch, an increase in egg size or a decrease in total reproductive effort (if it tends to increase survivorship of adult females). Which way is favoured will depend on environmental conditions and specific morphology.

GILLER (1984) proposed to divide biological communities in associations including all coexisting species of the same taxon. Coexisting populations of related species often exploit similar resources and adapt to the environment in a similar way. In such a case they might be unified in guilds (ROOT, 1967). Any association may include one or more guilds.

Still now, no unified methods of dividing communities into guilds exist and intuition plays an important role (SIMBERLOFF & DAYAN, 1991). If an area is composed of two or more types of biota (e.g. forest and grassland plots, etc.), the simplest way of outlining guilds is to unify all species attached to the same type of biota. Spatial preferences could be a good index of similarity in exploitation of the main resources (food, breeding sites, etc.).

Perhaps species of the same guild are similar not only in utilization of resources, but also in components of their life cycles, e.g. spawning mode. Connection between guild structure of associations and divergence of life cycles in coexisting species seems to be a poorly researched aspect of community ecology.

Six anuran species spread in Georgia appear to be a good example for investigation of this problem. They are sympatric in many localities. Nevertheless, they could be divided in two different guilds, according to their biotope preferences. Species of the first guild are strictly attached to forest during the terrestrial stage of their life. They form isolated, fully sympatric populations in the small mountain canyons. Species of the second guild prefer open places even in localities where wooded areas predominate. They form large populations in the river valleys, penetrating partly into the habitats of the first guild. The first guild includes *Rana macrocnemis*, *Bufo [bufo] verrucosissimus* and *Pelodytes caucasicus*. These species will be named here "Brown Anura" in accordance with their coloration, independent of their taxonomic position. The second guild includes *Rana ridibunda*, *Bufo viridis* and *Hyla arborea*, named here "Green Anura". A general description of the ecology of these species (except *B. viridis*) in Caucasus was given by TUNIYEV & BEREGOVAYA (1986).

The aim of the present investigation is the comparative analysis of spawning modes of these species. The study addresses the questions of which parameters of spawning may be common to species of the same guild but differ between guilds, and which parameters are variable within a guild

MATERIALS AND METHODS

The investigation was conducted in the Borjomi Canyon, Central Georgia. I studied amphibian habitats in the canyon of the river Nedzura (the right tributary of the river Kura). The stretch of the canyon from the mouth of Nedzura (where a village is located) to sources of the river exceeds 15 km (fig. 1). Elevation ranges from 900 to 1200 m. Annual precipitation amounts to 1000 mm. The river is framed by slopes covered with mixed forest (*Abies nordmanianna*, *Picea orientalis*, *Fagus orientalis*, *Carpinus caucasicus*). The total area of terrestrial habitats in the canyon reaches about 460 hectares.

About 100 rain pools and pool sites along creeks, ranging from 1 to 3-4 thousands liters, are used as anuran spawning sites. Size, temperature, lighting and flowing regime of the different water bodies vary considerably.

Observations were made during April-July 1989-1991. All water bodies were inspected on every second to tenth day. Numbers of deposited clutches of each anuran species were

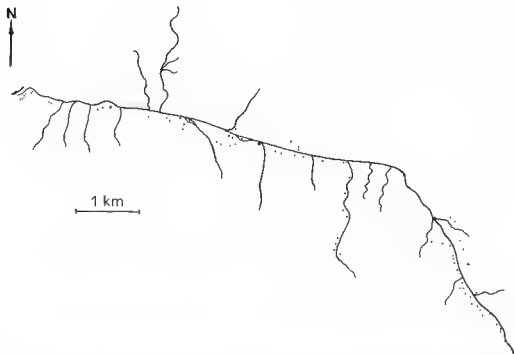


Fig. 1. Investigated part of the river Nedzura canyon (from the village to sources). Dots reflect the distribution of breeding sites

counted. The volume of each water body was estimated with the half-ellipsoid volume equation $v = \pi abc/6$. Tadpole number in all water bodies was estimated just before metamorphosis, at stages 40-41 (GOSNER, 1960). This number was used as approximate value of metamorphosed offspring. In some pools, the number of tadpoles was estimated visually. In other cases, up to 1000 tadpoles were stained in Neutral Red solution (GUTTMAN & CREASEY, 1973), released and recaptured 8-24 hours later. The total number of tadpoles was estimated with the Petersen method (CAUGHLEY, 1977). The number of pools where eggs or larvae were eliminated before metamorphosis was also counted.

Nineteen amplexed couples of *R. macrocnemis*, 21 of *P. caucasicus* and 29 of *B. verrucosissimus* were taken from spawning sites. Each couple was placed in a separate plastic box containing 3 l of stream water. After spawning, the following measures were taken: (1) body length (L = snout-urostyle length) of each female was measured to the nearest 0.1 mm, using callipers; (2) average diameter of 30 eggs in each spawn clutch (D) (for this aim, the outer envelope was removed from each egg before the first cleavage, eggs were transferred to petri dishes containing water; egg cell diameter was measured to an accuracy of 0.05 mm using a binocular with an eyepiece micrometer); (3) fecundity (N = number of eggs per clutch); in the small clutches of *P. caucasicus* eggs were counted directly, while for the large clutches of *R. macrocnemis* and *B. verrucosissimus* the

following procedure was applied: a portion of each clutch containing 200 eggs with their envelopes was removed and its volume was measured; the total volume of the clutch was also measured immediately and, thus, total egg number was calculated; ten females of each species were killed after spawning for further examination of their ovaries.

Eighty-four naturally deposited clutches of *R. macrocnemis*, ten clutches each of *H. arborea* and *B. viridis*, and five clutches of *R. ridibunda* were also studied. In these clutches, D was measured at stage 9 (GOSNER, 1960). Five females of *B. viridis* and *R. ridibunda* and three females of *H. arborea* were caught just after spawning, killed, and their ovaries were inspected.

Egg volume (mm^3), calculated as $v = D^3 \pi 6^{-1}$, was used instead of D in the basic calculations. The total volume of clutch V (ml) was calculated as Nv . For estimation of specific volume of clutch, in comparison with body size of female, I used the index $SV = VL^{-3}$.

Standard methods of correlation and regression analysis (ZAITSEV, 1984) were used for establishing connections between separate measures. For each data sample, the arithmetic mean M and the main statistical parameters were estimated. For each compared pair of samples, the correlation coefficient R was calculated. When interdependence between two groups of data could be described as linear, parameters of a linear regression $y = ax + b$ were estimated. When interdependence was clearly curvilinear, parameters of the allometric equation $y = ax^b$ or the hyperbolic equation $y = a \cdot bx^{-1}$ were estimated. Electivity of females to pools of different volumes was quantified using the electivity index of IVLEV (1961): $J = (P_1 - P_1^*) / (P_1 + P_1^*)$, where P_1^* is the percentage of water bodies of the given class in the environment and P_1 is the percentage of spawn clutches deposited in ponds of this class.

RESULTS

GENERAL DESCRIPTION OF SPAWNING MODES

Brown Anura breed in small water bodies in the forest area. *Rana macrocnemis* begins to spawn in early April, and the reproductive period lasts about two weeks. Females spawn in stagnant or seepage pools, seldom in slowly running creeks. Spawn is deposited as large clumps floating in water. *Pelodytes caucasicus* begins to spawn in May or early June, and the breeding period continues through October. It spawns in slowly running water bodies, rarely in stagnant pools. Spawn clumps are attached to aquatic vegetation or sunken objects. Larvae usually hibernate and metamorphose in the second year of their life. *Bufo verrucosissimus* begins to breed in April; the breeding period continues through June. It usually spawns in slowly running water bodies. Sometimes males wait for females in water as in other species, but more often mating takes place on land. Amplexing couples remain on the ground surface for up to one week, looking for appropriate breeding sites. If a satisfactory site is not found, females may spawn on the ground surface. Spawn is deposited in long cords. There were no visible oocytes in the ovaries of females of Brown Anura after spawning each female deposits a single clutch per year.

The main breeding sites of Green Anura are situated outside of the studied area, in the valley of river Kura. They are permanent ponds, often with rich vegetation. In the study area, Green Anura deposit spawn in warm rain pools. Breeding periods of all three species continue from mid-April to mid-July. *Bufo viridis* is the most indiscriminating in terms of breeding site selection. *Rana ridibunda* spawns only in the largest pools (500 l and more). Oocytes of different size were present in the ovaries of females of Green Anura having just spawned (except three females of *B. viridis*): probably each female deposits some egg portions during the breeding season. Mating occurs in water in all three species.

BODY LENGTH AND FECUNDITY

The body length (L) of breeding females is shown in Table I. It increases in the order *P. caucasicus* - *R. macrocnemis* - *B. verrucosissimus* in the Brown Anura guild. Average L of *B. verrucosissimus* exceeds body length of *R. macrocnemis* by a factor of 1.6, and the latter exceeds body length of *P. caucasicus* also by a factor of 1.6. Number of eggs per clutch (N) increases between species with body size: *R. macrocnemis* deposits 3.1 times more eggs on average than *P. caucasicus*, and *B. verrucosissimus* 4.1 times more than *R. macrocnemis* (Table I).

Fecundity also depends on body size within populations. N correlates with L in *R. macrocnemis* and *P. caucasicus*. The highest value of the correlation coefficient R_{LN} was found in *R. macrocnemis* perhaps as a result of the high variability in female body length: $R_{LN} = 0.709$ ($n = 19$, $P < 0.001$; $N = 38.5 L - 1267$). In *P. caucasicus*, the correlation coefficient was: $R_{LN} = 0.678$ ($n = 17$, $P < 0.001$; $N = 52.9 L - 1835$). Correlation of N and L in *B. verrucosissimus* was not significant: $R_{LN} = 0.232$, $n = 29$.

To test the assumption of a common allometric relationship, I estimated the correlation between the logarithms of N and L for a combined sample, including data of all three species. Correlation of logarithmic data was 0.962 ($n = 65$, $P < 0.0001$; $N = 0.0136 L^{2.73}$) (fig. 2).

BODY SIZE AND EGG SIZE

Species of the Brown Anura guild with larger body size have larger eggs (Table I). Moreover, correlations between L and D were found within populations. Correlation coefficients in *P. caucasicus* and *R. macrocnemis* populations were 0.669 and 0.800, respectively. Correlation coefficients of v and L were 0.684 and 0.704 (n respectively 17 and 19, $P < 0.001$ in both cases; in *P. caucasicus*, $v = 0.137 L - 3.62$; in *R. macrocnemis*, $v = 0.132 L - 4.60$). In the *B. verrucosissimus* population, egg size was not correlated with female body size: $R_{LV} = 0.121$.

If data for the three species are lumped together, a clear curvilinear connection between v and L appears. Correlation of logarithmic data is 0.772 ($n = 65$, $P < 0.001$). Empirically this connection could be satisfactorily described by the hyperbolic equation $v = 7.9 - 230.5 L^{-1}$ (fig. 3).

Table 1. - Reproductive characteristics of anurans inhabiting Borjomi Canyon. L: body length (mm); N: number of eggs in the clutch; D: diameter of fertilized eggs (mm); v: volume of eggs (mm³); SV: specific volume of clutch, $SV = VL^{-1}$, where $V = vN$; n: sample size; M: arithmetic mean; S: standard deviation; SE: standard error; CV: variation coefficient (%). Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*; Bve: *Bufo verrucosissimus*; Ha: *Hyla arborea*; Rr: *Rana ridibunda*; Bvi: *Bufo viridis*.

	n	M	S	SE	CV	Limits
Pc	21	44.64	2.13	0.46	4.8	40.5-48.0
Rm	19	71.50	6.62	1.52	9.3	53.3-79.0
Bve	29	113.74	4.85	0.90	4.3	102.6-123.5
Ha	5	51.9	0.63	0.28	1.2	51.3-53.1
Rr	20	98.8	2.63	0.59	2.7	92.7-105.2
Bvi	16	81.3	7.94	1.99	9.8	51.9-93.8
Pc	21	493	147	32	29.8	100-750
Rm	19	1513	377	87	24.9	750-2100
Bve	29	6145	1815	337	29.5	3100-10000
Pc	17	1.69	0.13	0.03	7.6	1.4-2.1
Rm	19	2.11	0.19	0.04	9.1	1.7-2.4
Bve	29	2.22	0.15	0.03	6.9	1.9-2.5
Ha	10	1.33	0.12	0.03	9.0	1.1-1.6
Rr	5	1.72	0.05	0.02	2.9	1.6-1.9
Bvi	10	1.36	0.10	0.02	7.2	1.1-1.6
Pc	17	0.0141	0.0040	0.0009	28.6	0.004-0.021
Rm	18	0.0184	0.0047	0.0012	25.7	0.010-0.032
Bve	29	0.0241	0.0097	0.0032	40.4	0.012-0.046

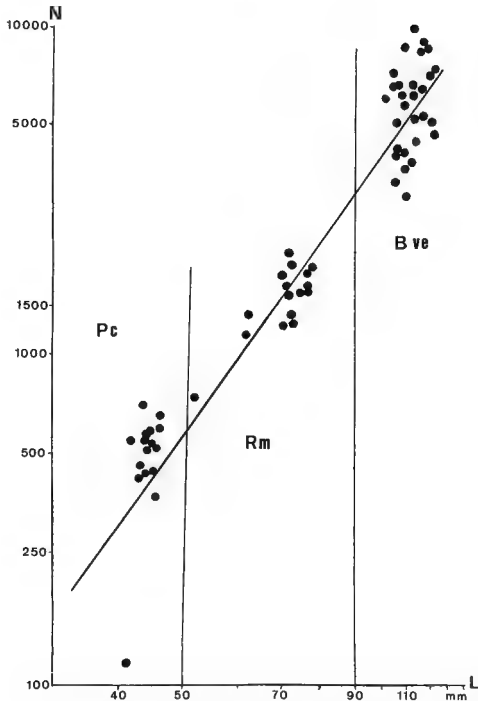


Fig. 2. — Correlation of egg number in clutch and body length of female (only for Brown Anura guild; logarithmic scale). N: egg number, L: body length (mm). Solid line reflects regression of N on L: $N = 0.0136 L^{2.732}$. Bve: *Bufo verrucosissimus*; Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*.

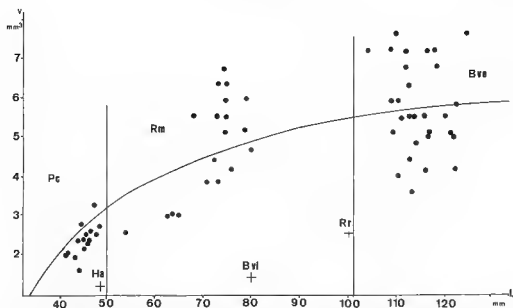


Fig. 3. — Correlation of arithmetic mean of egg size in clutch and body length of female. v : mean egg volume (mm^3), L : body length (mm). $v = 7.9 - 230.5 L^{-1}$. For Green Anura, only arithmetic means of values are shown. Bvs: *Bufo verrucosissimus*; Bvi: *Bufo viridis*; Ha: *Hyla arborea*; Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*; Rr: *Rana ridibunda*.

Eggs of Green Anura are smaller than eggs of Brown Anura for animals with similar body size (fig. 3). Egg size is related to female body size as in the Brown Anura guild. *Hyla arborea* has the smallest eggs, *R. ridibunda* the largest ones (Table I, fig. 3).

EGG SIZE AND FECUNDITY

No correlation between v and N was found within separate Brown Anura populations. For 84 naturally deposited *R. macrocnemis* clutches, correlation between v and N was 0.167, $P > 0.05$. Linear correlation between N and v exists at the across-species level ($R_{vN} = 0.947$, $P < 0.001$, $n = 84$, $v = 0.661 N - 0.027$). Common dependence of N and v on L provides the basis of this connection.

BODY SIZE OF FEMALE AND VOLUME OF CLUTCH

We can judge variability in volume of clutches only for Brown Anura. In *P. caucasicus* and *R. macrocnemis* populations, a positive correlation between L and V exists (0.862 and 0.828 respectively, $n = 17$ and 19, $P < 0.001$). Coefficients of linear regressions of V on L are 0.218 and 0.345 (fig. 4). In *B. verrucosissimus*, correlation of L and V is absent, R_{LV}

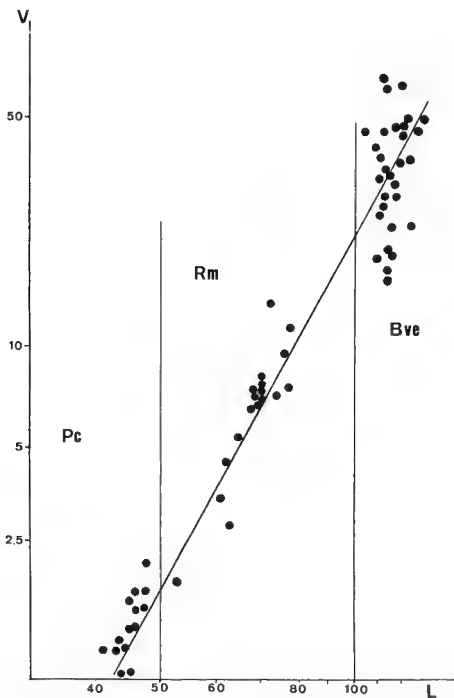


Fig. 4 — Correlation of body length and clutch volume in Brown Anura guild (logarithmic scale)
 $V = vN$ - clutch volume (ml), L : female body length (mm). $V = 0.00000171 L^{3.55}$. *Bve*: *Bufo verrucosissimus*; *Pc*: *Pelodytes caucasicus*; *Rm*: *Rana macrocnemis*.

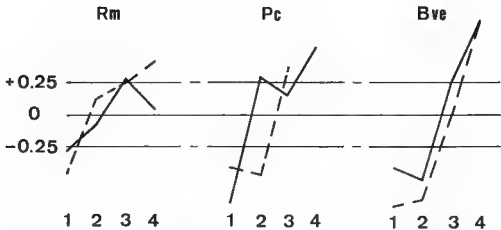


Fig 5. — Electivity of spawning sites of different sizes. Continuous lines. 1989, dashed lines: 1990 (1): water bodies of volume to 20 l; (2): to 160 l, (3) to 1280 l, (4) more than 1280 l Bve: *Bufo verrucosissimus*; Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*

— 0.123 Lumping together data of all three species, a curvilinear relation between L and V was obtained. Correlation of logarithmic values was 0.972 ($n = 64$, $P < 0.001$). The relation $V = 0.0000017 L^{3.6}$ (fig. 4) shows that clutch volume increases stronger than female body volume. The allometric relation of N and L is strengthened by a positive correlation between body size and egg size. For all three species taken together, there is also a positive correlation between SV and L: $R_{L, SV} = 0.501$, $n = 64$, $P < 0.001$, $SV = 0.141 L - 8.66$.

EXPLOITATION OF BREEDING SITES AND SPATIAL STRUCTURE OF ANURAN POPULATIONS

The number of available breeding sites appears to be the main factor limiting population numbers of anuran species. During 1989-1990, spawn was deposited in 188 small water bodies in the study area. The total number of clutches of Brown Anura species is presented in Table II. Most of the pools dried up or were washed off by rains before metamorphosis was completed. A few water bodies yielded emergence of most offspring (Table II). All Brown Anura species avoided the smallest water bodies and preferred the largest ones (fig. 5). As a result, spawning often took place in pools already populated with larvae of other species (Table III). In such cases, growth of younger tadpoles was retarded. Nevertheless, after metamorphosis of older larvae, growth and development of younger tadpoles renewed and they passed metamorphosis. As a result, even limited numbers of effective breeding sites in the canyon ensure quite high generation numbers in all Brown Anura populations.

The situation in Green Anura species is different. In the Nedzura canyon, their reproductive niches are included fully in the reproductive niche of *R. macrocnemis*. Large

Table II. - Egg and larval mortality in Brown Anura populations. 1: number of water bodies where spawning took place; 2: total number of clutches deposited in the canyon; 3: number of breeding sites where metamorphosis was completed; 4: number of clutches taking part in the formation of the new generation; 5: approximate number of tadpoles surviving to GOSNER stages 40-41 in all breeding sites of the canyon; 6: number of tadpoles in breeding sites with lowest mortality rates (the number of such water bodies is given in brackets); 7: survival rates from egg to metamorphosis in all sites (%); 8: survival rates in most effective breeding sites (%). Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*; Bve: *Bufo verrucosissimus*.

	1989			1990		
	Pc	Rm	Bve	Pc	Rm	Bve
1	46	56	17	28	89	17
2	410	362	49	331	1037	86
3	10	13	5	13	10	8
4	150	172	14	260	235	72
5	6000	15500	3500	6000	44500	45000
6	4000(1)	13073(2)	3000(3)	4000(1)	35703(3)	40000(1)
7	4.92	0.83	1.16	6.10	0.92	8.52
8	14.96	11.34	5.42	14.33	19.51	12.52

Table III. - Overlap of breeding sites explored by different Brown Anura species: the percentage of water bodies already populated with larvae of species B from all water bodies where spawning of species A took place. Bve: *Bufo verrucosissimus*; Pc: *Pelodytes caucasicus*; Rm: *Rana macrocnemis*.

A	B	1989	1990
Rm	Pc	27.3	13.7
Pc	Rm	16.7	75.2
Pc	Bve	17.4	15.5
Pc	Rm, Bve	21.5	84.8
Bve	Rm	14.9	18.9
Bve	Pc	53.2	17.2
Bve	Rm, Pc	65.9	23.1

tadpoles of this early-breeding species were present in almost all spawning sites of Green Anura. As a result, larvae of these species were usually eliminated already in early developmental stages. Emergence occurred only in pools which were not populated with Brown Anura larvae. Only a few offspring of Green Anura emerged during the year in the study area: some hundreds *B. viridis*, some tens *H. arborea* and a few specimens of *R. ridibunda*. This amount is not enough for renewal of Green Anura neighborhoods populating the canyon. These neighborhoods depend on immigrants from the river Kura canyon, where large permanent ponds are present and breeding is more efficient.

DISCUSSION

In boreal associations of Anura, species attached to wooded areas (brown frogs, *Bufo bufo* complex, etc.) often coexist with species preferring open plots (*Rana kl. esculenta* complex, green toad, etc.) (e. g. TUNIYEV & BEREGOVAYA, 1986; PIKULIK, 1985; etc.) Green frogs and green toads are most widely distributed, penetrating even into urbanized territories. "Forest" species are commonly early-breeders (BANNIKOV et al., 1977). In localities where forest areas predominate, they have an advantage in utilization of spawning sites due to well known priority effects (HEUSSER, 1972; PIKULIK, 1976; ALFORD & WILBUR, 1985; etc.). For example, *Rana sylvatica* tadpoles suppress *Hyla crucifer* tadpoles when they breed in the same ponds (MORIN & JOHNSON, 1988); *Rana temporaria* and *Bufo bufo* suppress development of *Bufo calamita* (HEUSSER, 1972; BANKS & BEEBEE, 1987; GRIFFITHS, 1991). In the association described here, "Green Anura" are weak competitors in small temporary pools, though species of this guild have wider possibilities of exploitation of large permanent ponds, most of which are situated in open areas.

On the other hand, hot and dry main terrestrial habitats of Green Anura are perhaps less favourable than humid forest habitats. As a result, Green Anura appear to be stronger competitors in the terrestrial stage of life whilst Brown Anura are stronger competitors during larval development.

The common spawning strategy of Green Anura species includes: diminishing of reproductive costs due to unfavourable terrestrial habitats; perhaps increasing fecundity in more predictable spawning conditions. Diminishing of reproductive costs is attained via asynchronous development of oocytes and portional spawning. Portional spawning is known for many species of Anura distributed in countries with a hot climate (see DUELLMAN & TRUEB, 1986, for review). Interestingly, *R. ridibunda* and *B. viridis* in northern parts of their range deposit a single clutch during the breeding season (e. g. KUBANTSEV et al., 1979; PIKULIK, 1985; GOROVAYA & DZHANDAROV, 1986). Increasing fecundity is attained at the expense of egg size. I have no information about the actual fecundity of Green Anura in the studied area, but fecundity of *H. arborea*, *R. ridibunda* and *B. viridis* was investigated in different regions by previous authors. Individual *H. arborea* females deposit 744.8 ± 45.5 eggs in Czechoslovakia (MORAVEC, 1989) and up to 1000 eggs in Ukraine (SCZERBAK & SCZERBAN, 1980). *Rana ridibunda* females deposit 4000-12000 eggs in different parts of this species' range (AVRAMOVA et al., 1976; KUBANTSEV et al., 1979; GOROVAYA & DZHANDAROV, 1986). A single full clutch of *B.*

viridis found in our study contained about 10000 eggs. In different regions, *B. viridis* females deposit 6000-14500 eggs (AVRAMOVA et al., 1976; KUBANTSEV et al., 1979). These values are significantly higher than those obtained for Brown Anura of comparable body size. Fecundity of brown frogs and common toads in Europe is also lower than estimates cited for *R. ridibunda* and *B. viridis* (GIBBONS & MCCARTHY, 1986; READING, 1986).

Allometric interdependence between N and L reflects the fact that N increases with body volume, not body length: $N = aL^b$, where $b \approx 3$. When $b < 3$, oocyte number increases slower than body volume; when $b > 3$, oocyte number increases faster than body volume. Interestingly, the general allometric index of the relation of N and L obtained for Brown Anura (2.73) is equal to an analogous value established for the grass frog *Rana temporaria* (GIBBONS & MCCARTHY, 1986). This species is ecologically rather similar to *R. macrocnemis*. Inversely, in the rice frog "*Rana*" *limnocharis* (characterized by portional spawning), this index is 3.47 (SHICHI et al., 1980).

Species spawning in small temporary pools have larger eggs and lower fecundity than related species which spawn in permanent water bodies (CRUMP, 1981, 1989; WOODWARD, 1987; RAFINSKA, 1991). Accordingly, eggs in Brown Anura species are larger than in Green Anura of comparable body size. Egg size increases with female body size more rapidly in this guild (fig. 3). Increase of egg size as well as increase of egg number per clutch are limited by female body size in both guilds. But among Green Anura, fecundity increases at the expense of egg size; in Brown Anura, egg size increases at the expense of fecundity.

An additional factor determining the equilibrium point between egg size and fecundity appears to be environmental temperature. Increase of temperature causes conservation of high fecundity at the expense of egg size in *Bombina orientalis* (KAPLAN, 1987). This dependence may be generalized to the interspecific level. Temperature in the main habitats of Green Anura species is higher than in the Brown Anura habitats.

Within Brown Anura, differences in spawning mode are connected with female body size. The choice of the way of adaptation is whether rapid maturation but a small clutch will be favoured or a large clutch but postponement of maturation. Smaller Brown Anura species mature in shorter time than larger ones (GOKHELASHVILI & TARKHNISHVILI, in prep.). Rapid maturation decreases the period between generations and increases the number of adult animals. On the other hand, body size remains small and fecundity low. Egg size is also limited. Larger Brown Anura species increase their reproductive effort at the expense of the period between generations.

The taxonomic position of a species is not connected with its position neither on the "macrohabitat" nor on the "body size" axes. Both pairs of congeneric species (*Rana* and *Bufo*) are divided among two different guilds.

BEGON et al.(1986) noted that interspecific differences of life cycles often deviate from the framework of the widely known r-K model. Perhaps the direction of the life cycle variation between any two species depends on their position in the guild structure of the community. For our case, species of the same guild vary both in fecundity and egg size but have a common relation between these characters and female body size. Species of different guilds have a different correlation between egg size, fecundity and female body

size. The main reason of interspecific differences within a guild appears to be species-specific body size, whereas between guilds environmental conditions in the main terrestrial habitats seem to be important

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